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**THE COMPARATIVE AGE OF THE DIFFERENT FLORISTIC ELEMENTS OF
EASTERN NORTH AMERICA.**

BY JOHN W. HARSHBERGER, PH.D.

The historic element must be considered in a phytogeographic study of any country. Many questions concerning the present distribution of plants depend upon the character and extent of the past distribution of the species of any region or formation. The degree of invasion of new species into a region is determined by the presence or absence of vegetation. If vegetation is present, then the botanist is compelled to account for its presence by a consideration of the physiographic history of that part of the earth's surface, the association of species and the probable origin of these species, whether indigenous or derived. The determination of the indigenous and derived species of a formation or larger division is of the utmost importance, as it enables us to retrace the steps by which the formation has reached its present condition and association of species, and to reconstruct formations that have long since disappeared.

The methods which must be adopted in scrutinizing the flora of a country are several:

1. The botanist must determine the past and present physiography of the region concerned.
2. He must determine, if possible, the geologic time at which the recorded physiographic changes took place.
3. He must recognize the indigenous species by eliminating the derived.
4. A study of the distribution of species will enable him to determine to some extent the age of the different floristic elements, and the application of the following criteria will also aid him in the solution of questions such as are considered here.
 - a. Location of greatest differentiation of type.
 - b. Location of dominance or great abundance of individuals.
 - c. Location of synthetic and closely related forms.
 - d. Location of maximum size of individuals.
 - e. Location of greatest productiveness and its relative stability.
 - f. Continuity and convergence of lines of dispersal.
 - g. Location of least dependence upon a restricted habitat.

h. Continuity and directness of individual variations, or modifications radiating from the centre of origin along the highways of dispersal.

i. Direction indicated by biogeographic affinities.¹

5. Old regions, botanically speaking, may be determined where the number of specific forms of single genera is small, and new regions may be determined where the number of species of single genera is ordinarily very large.

6. Drude's classification of endemic plants, as corresponding and as relict, is of great assistance to the botanist in determining the age of floristic elements. Plants are corresponding when the original continuous area of a variable species has been interrupted in such a way as to form several smaller areas occupied by subspecies or new species, while relicts are those species originally of extensive distribution able to maintain themselves in a limited area only on account of changed conditions of life. Having enunciated these general principles, I will endeavor to apply them in the determination of the age of the different floristic elements of eastern North America.

All of eastern America north of the great terminal moraine which marks the southern boundary of the great ice sheet, with the exception of the nunataks, has been tenanted by plants which have migrated into the territory abandoned by the great continental glacier. Geologists believe, from evidence afforded by the time that it has taken for the river to cut the gorge at Niagara, that 10,000 or 15,000 years have elapsed since the close of the glacial period. If their deductions are sound, then the flora of the northern part of eastern America cannot be older than 15,000 years at the outside. Some of its elements may be much older, and we have reason to believe that many boreal plants existed as such on the nunataks, which were unglaciated areas above the great ice sheet. The first wave consisted of the distinctly glacial flora, which skirted the border of the ice sheet. The second wave, younger as a floristic element of the North, consisted of boreal plants, many of which, as bog plants, tenanted the bogs and margins of the glacial lakes that were formerly much more abundant in the North than at present. These bog and tundra types pushed early into the barren ground left by the retreating ice. The tundra was closely followed by the coniferous forests on the western and eastern sides of the glaciated areas and these trees constitute a third floristic element, much younger in point of the time in which they have occupied the North. These trees, and those forming a still younger element, surrounded the bog plant societies which were trapped by the surround-

¹ ADAMS, CHAS. C., *Biological Bulletin*, III : 122.

ing tree vegetation, and as the bog was gradually transformed by biologic influences into firmer ground gradually encroached on the bog plant associations. Present bog habitats are continuations of similar habitats which existed in early postglacial times, when tundra conditions and tundra vegetation were dominant.² The fourth element just mentioned consisted of deciduous shrubs and trees, oaks, hickories and the like, which at present are south of the great coniferous belt of forest. In the East, among the highlands, exceptional circumstances were afforded for the preservation of the northern forms.

The flora of Mount Washington is perhaps an exception to this. During the glacial period it was a nunatak, and during this time it was tenanted by such plants as *Silene acaulis* L., *Arenaria grænlandica* Spreng., *Geum radiatum* Michx., *Solidago virga-aurea* L. var. *alpina* Bigel., *Prenanthes bootii* Gray, *Cassiope hypnoides* Don, *Bryanthus taxifolius* Gray, *Diapensia lapponica* L., *Oxyria digyna* Hill, *Salix phyllifolia* L., *Salix uva-ursi* Pursh, *Salix herbacea* L., *Phleum alpinum* L., *Lycopodium selago* L., etc., which have remained as permanent tenants of this mountain. If we take Mount Washington as a mountain, the summit flora is older than that of the lower alpine slopes of the mountain above timber-line, and the flora, therefore, of these slopes is in turn older than that of such gorges as Tuckerman's Ravine, Huntingdon Ravine and Great Gulf, which probably supported local glaciers for many centuries after the great ice sheet had retreated from the Presidential Range.

Mount Katahdin, 161 miles northeast of Mount Washington, has a less number of alpine plants than that mountain, and most geologists believe it to have been buried entirely beneath the glacial ice sheet. If that is so, then the alpine flora of Mount Katahdin is, as a floristic element, much younger in point of time than that of Mount Washington. The same differential arrangement of the plants on Mount Katahdin is found as on Mount Washington. The place where the boreal flora, upon the retreat of the continental ice sheet, encroached upon Mount Katahdin is determined largely by the physiography of the mountain. The glaciers occupying the various basins of the mountain retarded the revegetation of the mountain, but with a favorable opportunity the encroachment perhaps began from the southwest and west. This idea seems to be confirmed by the present distribution of the spruce and fir which ascend higher on this side and their apparently greater age. As to the east side of the mountain,

²TRANSEAU, E. N., *Botanical Gazette*, XXXVI: 401.

and in particular the basins, it seems probable that the great basin³ was first tenanted by plants, and that the North Basin opposed this migration a much larger time for the reason that this basin, which presents a scene of desolation, was the seat of a local valley glacier which was, perhaps, the last to disappear. As a consequence, the basin presents an appearance even more xerophytic and alpine than some of the upper parts of the mountain itself. The pucker bush (*Krummholz*) reaches here an unusual development, with the trees lying in most places prostrate and gnarled and twisted to a high degree.

The swamp societies of the northern America stand in contrast to the bog societies made up of more southerly forms, and must be considered to be the normal hydrophytic vegetation of present climatic conditions. The swamps of the North have had a much later origin than the bogs, for we find that if the depressions provided with water have existed since the days of the tundra they may show a bog flora to-day; if they are of recent origin the plants will correspond to the normal swamp plants of the present climatic conditions.

Another interesting problem which presents itself is that of the presence of typical seashore plants on the coasts of the Great Lakes. Such plants as *Ammophila arundinacea* Hast., *Sabbatia angularis* Pursh, *Lathyrus maritimus* Bigel., *Hudsonia tomentosa* Nutt., *Cakile americana* Nutt., *Hibiscus moscheutos* L., *Gerardia purpurea* L., *Euphorbia polygonifolia* L., *Myrica cerifera* L., *Strophostyles peduncularis* Ell. are found not only on the shores of the Great Lakes, but some of them near the Lake of the Woods. The most satisfactory explanation seems to be that in post-glacial times the valleys of the St. Lawrence, Hudson, Lake Champlain, and probably also Lakes Ontario and Superior, were then occupied by the sea, because of the northeasterly depression of the land. During this period of submergence the typical seashore plants gained access to the interior of the continent.

The country south of the great ice sheet shows some interesting problems of geographic distribution in line with the subject of this paper. The northward extension of the pine barren flora on Long Island and Staten Island is a case in point.⁴

The soil of the region is generally sandy, but is occasionally more firm where strata of clay approach and form the surface. The geological formations to the south and southeast of a line drawn from a point below Long Branch to another near the head of Delaware Bay

³ HARVEY, L. H., "A Study of the Physiographic Ecology of Mount Katahdin, Maine," *University of Maine Studies*, No. 5, December, 1903.

⁴Cf. N. L. BRITTON, on the "Northward Extension of the N. J. Pine Barren on Long and Staten Islands," *Bulletin Torrey Botanical Club*, VII, 81, July, 1880.

are Tertiary, while those to the north of it are Cretaceous. The Tertiary soils extend southward along the Atlantic to Florida. As the soil over both the Cretaceous and Tertiary is composed of similar materials, it is impossible to say, from surface indications, where one ends and the other begins. We will deal with the flora of the northern extension of these sandy stretches of Cretaceous age. On Staten Island these strata are exposed in its extreme southern portion. They doubtless extend over the entire southern and eastern sections, but are mostly covered by a layer of material of variable thickness derived from the glacial drift. On Long Island, the great terminal moraine occupied a position marked by a range of hills extending throughout its whole length at an average distance of ten miles from the Atlantic. South of these hills sandy plains prevail, the material composing them having been formed partly from the modified drift of the hills, partly from the underlying Cretaceous strata. Those species detected on the Cretaceous soils of Staten Island, and not on the drift, are thirty-four in number: *Magnolia glauca* L., *Hudsonia ericoides* L., *Ascyrum crux-andree* L., *Arenaria squarrosa* Mich., *Polygala lutea* L., *Tephrosia virginiana* Pers., *Desmodium laevigatum* D. C., *Desmodium viridiflorum* Beck, *Rubus cuneifolius* Pursh, *Crataegus parvifolia* Ait., *Eupatorium rotundifolium* L., *Aster nemoralis* Ait., *Aster concolor* L., *Chrysopsis mariana* Nutt., *Gnaphalium purpureum* L., *Gaylussacia dumosa* J. and G., *Andromeda mariana* L., *Kalmia angustifolia* L., *Ipomæa pandurata* Meyer, *Phlox subulata* L., *Asclepias obtusifolia* Michx., *Euphorbia ipecacuanhæ* L., *Quercus nigra* L., *Quercus prinoides* Will., *Quercus phellos* L., *Spiranthes simplex* Gray, *Juncus scirpoides* Lam. var. *macrostemon*, *Xyris flexuosa* Muhl., *Cyperus cylindricus* N. L. B., *Stipa avenacea* L., *Glyceria obtusa* Tin., *Panicum verrucosum* Muhl., *Andropogon macrourus* Michx., *Lycopodium inundatum* L. var. *bigelovii* Tuck. Of these the following four have been detected in Suffolk County, Long Island: *Desmodium viridiflorum* Beck, *Rubus cuneifolius* Pursh, *Ipomæa pandurata* Meyer, *Phlox subulata* L. In addition to the above list, however, the following sixteen additional species have been detected in Suffolk county, Long Island: *Drosera filiformis* Raf., *Ascyrum stans* Michx., *Eupatorium hyssopifolium* L., *Eupatorium leucolepis* T. and G., *Eupatorium album* L., *Aster spectabilis* Ait., *Solidago puberula* Nutt., *Chrysopsis falcata* Ell., *Helianthus angustifolia* L., *Coreopsis rosea* Nutt., *Utricularia subulata* Le Conte, *Cupressus thyoides* L., *Juncus pelocarpus* E. Meyer, *Xyris caroliniana* Walt., *Eleocharis melanocarpa* Torr., *Sporobolus serotinus* Gray. Thus it appears that thirty-four of these characteristic pine

barren plants grow in the southern part of Staten Island, and that forty-six of them have been detected in Suffolk county, Long Island.

It would seem that these species have a tendency to follow the course of the two more recent geologic formations throughout their whole extent along the Atlantic coast. Another fact which stands out prominently in this connection is that not a single one of the above-mentioned plants, growing, as we have seen, along the edge of the glacial drift, is native of Europe, but belong to a true American flora, which had its origin in the southern part of the continent and migrated northward into Staten Island and Long Island at the close of the great ice age. In contrast to this fact we have another one, equally prominent, and that is, that of the species of plants growing on the morainic material about one-third are common to northern Europe and America, thus pointing to a common origin of each in the territory now occupied by the ice and snow of the Arctic regions. The flora north of the morainic line in Staten Island and Long Island clearly antedates in point of occupancy of the country the more southern and American pine barren flora, which migrated northward at a date subsequent to the migration of the flora with strong European affinity.

Another interesting illustration of the historic factors instrumental in plant distribution is afforded by the peculiar flora of the Kittatinny or Shawangunk mountains of northwestern New Jersey. This mountain chain forms a wall of almost constant altitude, averaging over 1,200 feet in height, along the eastern side of the Delaware river from Port Jervis to the Delaware Water Gap. Its summits and western slopes are composed of a coarse or fine, very hard silicious conglomerate or sandstone, with little soil but that derived from the limited disintegration of these rocks, and it is therefore highly silicious. While the mountain sides are extensively glaciated there is very little glacial drift on the ridge.

On these mountains exist a number of plants which are also found in great numbers in sandy soil along the Atlantic coast. Among the species which are thus noteworthy, as discovered by N. L. Britton, are: *Juncus greenii* Oakes and Tuckerm., *Solidago puberula* Nutt., *Orontium aquaticum* L., *Tephrosia virginiana* Pers., *Lespedeza hirta* Ell., *Lupinus perennis* L., *Quercus ilicifolia* Wang., *Corema conradii* Torrey. At Culver's Gap were found by Britton: *Polygala polygama* Walt., *Gerardia pedicularia* L., *Lechea racemulosa* Michx., all abundant in sandy soil along the coast, and *Prunus pumila* L. At Sunfish Pond, northwest of the Water Gap, occur *Juncus militaris* Bigel., *Lycopodium inundatum* L., *Viburnum nudum* L. While all along the mountains grow

Aster linariifolius L., *Quercus ilicifolia*, *Gaylussacia resinosa* Tott and Gray, *G. frondosa* Torrey and Gray, *Vaccinium vacillans* Sol., *Epigaea repens* L., *Gaultheria procumbens* L., *Cassandra calyculata* Don and *Rhododendron viscosum* Torrey. Another peculiarity is the substitution of *Pinus rigida* Mill on the mountains for the *Pinus strobus* L. of the surrounding country.

The ridges of the Green Pond system, known at Greenwood Lake as Bearfort and Bellvale mountains, and in New York as the Skunne-munk, have a somewhat similar summit flora, consisting of *Quercus ilicifolia* Wang., *Solidago puberula* Nutt., *Tephrosia virginiana* Pers., *Lespedeza hirta* Ell., *Arctostaphylos uva-ursi* Spreng, *Aster linariifolius* L., various huckleberries, blueberries and other sand plants.

The reason for the somewhat remarkable similarity of the pine barren and summit mountain floras is usually attributed to the similarity of the soil on the mountains to that of the plains bordering the coast. It is probably true that the plants occupy these areas because they have adapted themselves to growing in soils of silicious sands, but to say that the soil is the prime factor in their distribution is putting the case too strongly. The writer believes, from an investigation that he has made of the problems involved, that the flora of the mountains is peculiarly an endemic one, showing relict endemism, and that the flora of the pine barren is a derived one, and is an illustration of Drude's principle enunciated above. The crest of the Kittatinny Mountains represents the level of a plain that existed prior to the great period of erosion which carved out the mountain ranges and has been several times elevated and depressed. During the period of its more extensive plain character, the plants above mentioned were distributed over the area now represented by the crests of the Shawangunk Mountains in New Jersey and the Skunnemunk Mountains in New York. With the wearing away of the plain this more ancient flora remained in a relict form on the summits of the mountains mentioned. This antedated many years the upheaval of the New Jersey coast plain, which was, after its appearance above the surface of the sea, an open field for the migration of plants from nearby formations. The pioneers into the elevated coastal plain were those species nearest at hand and most mobile and, by reason of occupancy of a similar soil, well adapted to meet the new conditions of environment. If we apply these principles to the problem in hand, we naturally reach the conclusion that certain plants of the coastal flora are derived from the formations nearest at hand which present similar environmental conditions, and are, therefore, for the coastal region comparatively new, so that the summit

flora of the mountains may be looked upon as relatively older in point of time than that occupying the territory along the sea coast.

An interesting confirmation of this position is found in a study of the succession of the floras on the Pocono Mountain plateau, following the destruction of the original forest by lumber operators. The original vegetation of this plateau consisted, as far as I have been able to determine, of four elements, viz.: a forest of pitch pine, *Pinus rigida* Mill., which covered the looser morainic material of the great terminal moraine in the eastern and southern parts of the plateau; the broad-leaved deciduous forest with its oaks and associated species on the eastern slopes and edge of the tableland; the chestnut and black locust forest which occupied Laurel Ridge along the western rim of the plateau, and a forest of white pine with a thicket of *Rhododendron maximum* L. beneath, mixed in many places with the black spruce, *Picea nigra* Link, the red maple and other plants characteristic of the Catskill mountains and farther north, grading over to a hemlock forest in the region of Tobyhanna. The open sphagnum bogs culminated in the presence of the larch, *Larix americana* Michx., with which were associated *Kalmia glauca* Ait., *Ledum latifolium* Ait., *Rhododendron rhodora* Don, and other northern plants. With the destruction of the white pine, hemlock and pitch pine forests, the vegetation of this tableland has undergone an entire change. The succession of the species has not been worked out in detail, but what has been observed is instructive. The botanist is impressed by the general appearance of the landscape. The flora over the eastern half of the plateau in aspect resembles that of the pine barren regions of southern New Jersey, from which the original pitch pine and Jersey pine have been cut. A study of the species shows that this appearance is due to the close similarity of the flora in the plant species which constitute the two regions. We have an instructive example of mass invasion of such plants as *Quercus ilicifolia* Wang., *Pinus rigida* Mill., *Gaylussacia resinosa* Torr. and Gray, *Vaccinium vacillans* Solander, *Epigaea repens* L., *Gaultheria procumbens* L., *Rhododendron viscosum* Torr., *Kalmia angustifolia* L., *Lilium philadelphicum* L., *Amianthium muscatoxicum* Gray, *Lycopodium inundatum* L., etc., from the morainic hills westward into the region occupied by the white pines. We naturally inquire from what locality the pitch pine formation has proceeded, and it seems to me we are forced to conclude that this association of species has been derived, not from the barrens of New Jersey, but from the nearby mountains northwest of the Delaware Water Gap which, as previously mentioned, support such a flora. This relict flora on the Kittatinny and other

highlands has been under unusual stress of circumstances, and when more favorable, but on the whole similar, edaphic conditions were supplied, a mass invasion from these mountain highlands took place at two different and widely divergent periods of time in two directions. After the uplift of the Jersey pine barrens region, the nearby flora of the upland plateaus being edaphically better adapted to the new region, supplied the barren ground with a vegetable covering. Similarly, when the glaciers retreated a mass invasion of pitch pines and associated species moved from the unglaciated Kittatinny Mountains on to the sandy gravelly soil of the great moraine, and when the lumbermen disturbed the forest these plants, adapted to growing in sandy soils and exposed to xerophytic conditions, supplied the constituent elements of the present flora in the greater part of the eastern half of the plateau.

A consideration of the strand flora of New Jersey, upon which I have spent considerable study, reveals the fact that the time element is important in an explanation of the distribution of the seashore plants. If we contrast the character of the association on the northern and southern shore of New Jersey, we find that the formations on Barnegat beach, for example, are usually open, while those on Wildwood beach are closed and have culminated in the forest type of vegetation. This argues for a greater age of the strand flora of Wildwood, as compared with that, for example, at Sea Side Park in the north. This conclusion is substantiated by the fact that the bays behind the sandy sea islands are converted into salt marshes in the south, while in the north they are wide and still open bays of brackish or salt water. Physiographically and botanically the coast line from Bay Head south to Ocean City is younger than the coast south of the latter place extending to Cape May.

The latest periods of submergence and uplift had a powerful influence on the distribution of sea-coast species. The present distribution of the swamp rose-mallow, *Hibiscus moscheutos*, in the Atlantic coastal plain illustrates this. The plant normally occurs in brackish marshes from Massachusetts to Florida and Louisiana and on lake shores in saline situations locally in the interior to western Ontario. When it occurs in fresh-water swamps it is reasonably certain that these swamps represent a converted salt marsh present during a former time of submergence. New Jersey shows this best. During the Pensauken submergence southern central New Jersey was an extensive sea island separated from northern New Jersey by Pensauken Sound. *Hibiscus moscheutos* in its present distribution in New Jersey follows the former

shore line of that ancient island, for it occurs in the salt marshes of the coast, on both banks of the Delaware river to the head of tide water, and also in fresh-water marshes along the New York Division of the Pennsylvania Railroad between Trenton and Newark, the roadbed between these cities being laid upon the geologic site of the Pensauken Sound.

South of New Jersey the region, including southeastern Pennsylvania, may be divided historically according to the age of the flora into several well-marked divisions.

1. The flora of the Southern Appalachians and its northeastern extension into southern and southeastern Pennsylvania. The facts presented in two former papers⁵ all argue for the great antiquity of the flora of North Carolina and southeastern Pennsylvania, because this flora, in all probability, represents the more or less modified descendants of that characteristic flora which in later Eocene or Miocene time extended to high northern latitudes.

2. The flora of the coast plain occupied by the long leaf pine with its associated species, which probably represent the ultimate stages of successions initiated at the time of the final elevation of the sea bottom along the coast line. These plants probably entered the elevated coastal region by a mass invasion from a circumscribed area contiguous to the Atlantic shore line, for it has been established that contiguous vegetation furnishes 75-90 per cent. of the constituent species of an initial formation. The reason for this is to be found not only in the fact that adjacent species have a much shorter distance to go and hence will be carried in greater quantity, but also in that species of the formations beyond must pass through or over the adjacent ones. In the latter case, Clements states that the "number of disseminules is relatively small on account of the distance, while invasion through the intermediate vegetation, if not entirely impossible, is extremely slow, so that plants coming in by this route reach the denuded area only to find it already occupied."⁶

3. Plants of probable Neotropic origin which have, according to Kearney, in all likelihood made their first appearance in the Appalachian region in geologically very modern times, probably after the close of the so-called glacial epoch.

⁵ HARSHBERGER, J. W., "An Ecologic Study of the Flora of Mountainous North Carolina," *Botanical Gazette*, XXXVI, 241-258, 368-383, 1903, and "A Phytogeographic Sketch of Extreme Southeastern Pennsylvania," *Bulletin Torrey Botanical Club*, XXXI, 125-159, March, 1904.

⁶ CLEMENTS, FREDERICK E., "Studies of the Vegetation of the State, III.—The Development and Structure of Vegetation," *Botanical Survey of Nebraska*, 1904.

4. A relict flora of a former widespread plateau region, similar to the one mentioned for northeastern Pennsylvania, in which we find a close similarity between the flora of some of the higher mountain summits and the flora of the coastal plain. We have previously mentioned in the physiographic changes which have taken place in this mountain region an explanation of such peculiarities of distribution. The presence of *Hudsonia montana* Nutt. on the summit of the Table Rock is probably thus explained, for Table Rock represents an undenuded remnant of a former peneplain. It is likely, therefore, that *Hudsonia montana* Nutt. was once more extended in its distribution, but has been isolated by the erosion of the plain on which it formerly grew in abundance. The presence of *Leiophyllum buxifolium* Ell., *Xerophyllum asphodeloides* Nutt., *Amianthium muscætoxicum* Gray on the mountain summits and on the coastal plain is also similarly explained.

5. The distribution of plants in the southern extremity of Florida is an interesting confirmation of the historic development of a flora. Seven plant formations can be recognized, viz.: (1) The sea-strand formation; (2) The mangrove swamp formation; (3) The everglade formation; (4) The grassland ("prairie") formation; (5) The savanna formation; (6) The pine-land formation; (7) The hummock-land formation. Historically the sea-strand formation and the hummock-land formation are the oldest, floristically speaking. The strand flora, consisting of such plants as *Uniola paniculata*, *Panicum amarum*, *Ipomœa pes-capræ*, *Batatas littoralis*, *Iva imbricata*, *Cakile maritima*, *Agave decipiens* (ontropic section), has existed as an element of the flora of peninsular Florida since the land was elevated above the sea, and perhaps was derived from an earlier seashore flora which existed along the shore of the mainland or the coasts of the larger and more elevated sea islands.

Nearly all the tropic species recently added to the flora of the United States were discovered in or about the hummocks, which are essentially duplicated by similar formations in the West Indies. The total area of the hummock-land is relatively insignificant when compared with the pine-lands, yet the flora, as shown in the enumeration below, is as rich, if not comparatively richer:

Pine-lands,	43 per cent.
Hummocks,	42 "
Everglades,	15 "

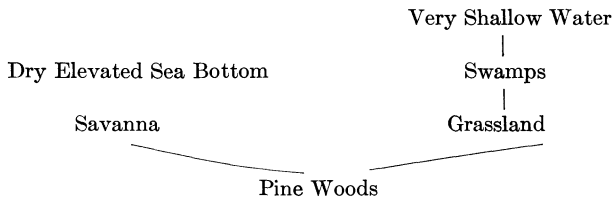
The hummocks consist of isolated groups of hardwood trees, shrubs and vines. These hummock formations with an overlying soil thicker than the pine-lands, due without doubt to the accumulation of vegetal

detritus, vary in size from an acre to many hundred acres, and are scattered as islands in the everglades and pine forests instead of surrounded by the ocean, as they formerly were before the sea bottom between them became dry land by elevation. The trees, shrubs and woody vines harbor an almost incredible growth of plants of various categories. The growth of epiphytes is especially striking, for in numerous cases the tree trunks and branches are completely clothed with air plants, and so prolific are the orchids and bromeliads that many individuals are forced to growth on the ground and on the neighboring pine trees.⁷ Here occur the great majority of flowering plants now known to be common both to the West Indies and the mainland of North America. As the rock of New Providence Island, of the Bahama group, is essentially identical with that of the Florida south of Miami, and as there are many trees and shrubs common to the two regions, as well as to Cuba, while many species are endemic to each of the three regions, we are forced to conclude from the evidence that the flora gives that geologically and to a certain extent floristically the hummock-lands formed originally part of the Antillean region. The hummock-lands, perhaps, represent part of the ancient system of Keys which existed at the time when the Gulf Stream left the American Mediterranean through a channel which existed across the northern half of Florida. It was when these islands formed an extended archipelago coextensive with the Bahamas that the hummocks were occupied by their present flora, which, therefore, shows the closest relationship to that of the nearby Bahama islands. With the elevation of the land through the epirogenic movements of the earth's crust, through the agency of coral polyps, vegetation, ocean and wind currents, the Gulf Stream was directed into its present channel and the sea islands which now exist in south Florida in the form of hummocks were connected by dry land or by partially submerged banks to form the present peninsula of Florida.

With the appearance of level plains by the removal of the shallow sea over a sandy bottom, the isolated trees and herbaceous plants which associated together constitute the savanna formation appeared and clothed the ground. Imperceptibly these savannas were transformed by the appearance of trees into the pine-land formation. This formation is characterized by a scattering growth of *Pinus heterophylla*

⁷ Consult the articles by J. K. SMALL, and N. L. BRITTON, in *Journal New York Botanical Garden*, III, No. 26, February, 1902; IV, No. 39, March, 1903; V, No. 51, March, 1904; V, No. 55, July, 1904; V, No. 56, August, 1904, to which the writer is indebted for many facts herein set forth under the new cloak of generalization.

and numerous shrubs, shrubby herbs and herbaceous perennials, together with a few annuals. Four species of palms belonging to the genera *Sabal*, *Serenoa*, *Coccothrinax*, and the Sago palm, *Zamia floridana*, are prominent representatives of the pine-land formation. These pine-lands are light and airy, with comparatively thin soil. The growth of timber is scattered and the plants found in this formation are not duplicated in the West Indies. Relatively, then, the flora of the pine-land formation is younger than that of the hummocks, and may be older or younger than the everglade formation, according to whether this association of species encroached on elevated plain land or whether it captured grassland or an everglade formation. The evolution of the pine woods may be represented for sake of clearness diagrammatically as follows:



The culmination from either condition has been a pine forest.

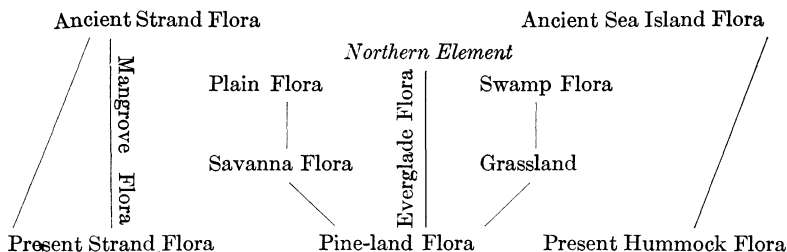
The everglades, then, historically speaking, may be older than the pine woods, or they may be younger. Whatever their position in point of time, they cover an area of about one hundred miles wide and perhaps one hundred and fifty miles long, the elevation being about eighteen feet above sea-level. This area consists of an extended saw-grass swamp traversed by winding river channels, and covered with scattered hummock-lands. Its flora consists of grasses, sedges and other herbaceous plants, among which are many aquatic and mud-inhabiting plants. The vegetation of the everglades is of a more northern character than that of the hummock-lands.

The mangrove formation represents an important element in the flora of southern Florida. The mangrove swamps are particularly abundant along salt or brackish shores and along the sea islands, the so-called Florida Keys.⁸ Their vegetation is confined almost exclusively to the mangrove trees and such few *Tillandsias* and orchids as grow upon their branches. Frequently on the borders of these swamps occurs a large showy species of *Acrostichum* with leaves often six to eight feet long. The area shut off from the sea by the fringe of man-

⁸ PHILLIPS, O. P., "How the Mangrove Tree adds New Land to Florida," *The Journal of Geography*, II, 1-14, January, 1903.

groves becomes dry ground and eventually grassland (in Florida "prairie").

The results of this survey as to the southern extremity of Florida may be arranged below:



Lastly are the ruderal plants and weeds that, introduced by the hand of man, have become established in America. The history of the introduction and spread of many of these plants is known to an exactness, whereas many have appeared and become established the history of which is involved in considerable doubt. The time which has elapsed since the advent of these outsiders does not exceed two or three hundred years, and yet in that time many American varieties of common European plants have by mutation or otherwise arisen to demarcate the American from the European forms.

I have endeavored to present in this paper the fact that the component elements of the flora of eastern North America have had an historic development, and I have attempted to give the methods of determining their relative or comparative age, as well as the philosophic reasons underlying their distribution. The outcome of these observations may be tabulated and arranged as follows, the top of the table representing the oldest elements of our flora:

CHART ILLUSTRATING COMPARATIVE AGE OF THE DIFFERENT FLORISTIC ELEMENTS IN THE FLORA
OF THE EASTERN NORTH AMERICA.

Old Sea Coast Flora			Great Miocene Flora	
Hummock-land Flora of Florida		Southern Plateau Flora	Appalachian and Piedmont Floras	Arctic Flora
			Forest Flora	Northern Plateau Flora
Tundra Bog Flora		(i) Summit Coniferous Forest, (ii) Deciduous Forest of Slopes		
(Southern) Present Sea Coast Flora of the At- lantic States (Northern)		Interglacial Arctic Flora		
		Pine Barren Element in New Jersey		
First Floral Wave into Barren Land North of Terminal Moraine		Present Flora of Alpine Summits of Mountains		
		Second Floral Wave into Barren Land north of Terminal Moraine and higher Mountains of Pennsylvania, New York and New England, including original Pocono Flora		
Modern Bog Flora		Third Floral Wave into Barren Land north of Great Terminal Moraine		
Neotropic Element	Modern Swamp Flora	Modern Pocono Flora		